

1 **Seabirds enhance coral reef productivity and functioning**
2 **in the absence of invasive rats**

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27 **Biotic connectivity between ecosystems can provide major transport of organic**
28 **matter and nutrients, influencing ecosystem structure and productivity¹, yet the**
29 **implications are poorly understood due to human disruptions of natural flows². When**
30 **abundant, seabirds feeding in the open ocean transport large quantities of nutrients**
31 **onto islands, enhancing the productivity of island fauna and flora^{3,4}. Whether leaching**
32 **of these nutrients back into the sea influences the productivity, structure, and**
33 **functioning of adjacent coral reef ecosystems is not known. Here, we address this**
34 **question using a rare natural experiment in the Chagos Archipelago, where some**
35 **islands are rat-infested, while others are rat-free. We found that seabird densities and**
36 **nitrogen deposition rates are 760 and 251 times higher on islands where humans have**
37 **not introduced rats. Consequently, rat-free islands had substantially higher $\delta^{15}\text{N}$**
38 **values in soils and shrubs, reflecting pelagic nutrient sources. These higher values of**
39 **$\delta^{15}\text{N}$ were also apparent in macroalgae, filter-feeding sponges, turf algae, and fish on**
40 **adjacent coral reefs. Herbivorous damselfish on reefs adjacent to the rat-free islands**
41 **grew faster, and fish communities had higher biomass across trophic feeding groups,**
42 **with overall biomass 48% greater. Rates of two critical ecosystem functions, grazing**
43 **and bioerosion, were 3.2 and 3.8 times higher adjacent to rat-free islands. Collectively,**
44 **these results reveal how rat introductions disrupt nutrient flows among pelagic,**
45 **island, and coral reef ecosystems. Rat eradication should be a high conservation**
46 **priority on oceanic islands, likely to benefit terrestrial ecosystems and enhance coral**
47 **reef productivity and functioning by restoring seabird derived nutrient subsidies from**
48 **large areas of ocean.**

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52 The flow of organic matter and nutrients among ecosystems is a major determinant of
53 productivity, composition, and functioning. Animals, such as moose⁵, salmon⁶, and sea
54 turtles⁷, can connect ecosystems by vectoring organic matter and nutrients between them.
55 However, the magnitude and implications of these natural dynamics are poorly understood in
56 contemporary ecosystems where humans have disrupted connectivity by creating barriers
57 such as dams, removing biomass, and introducing predators^{2,8}. Seabirds are globally
58 important drivers of nutrient cycling⁹, transferring nutrients from their pelagic feeding
59 grounds to islands where they roost and breed^{1,10}. This input of nutrient-rich guano increases
60 plant biomass, alters plant species compositions, and enhances the abundance of many types
61 of biota^{3,4}. Nutrients can leach from guano to adjacent marine systems, which may bolster
62 plankton densities and influence feeding behaviour of manta rays^{11,12}. However, the effects of
63 seabird transported nutrients on the productivity, structure, and functioning of highly diverse
64 coral reefs is currently unknown. Understanding natural nutrient connectivity is particularly
65 important, yet challenging, because invasive predators such as rats and foxes have decimated
66 seabird populations within 90% of the world's temperate and tropical island groups⁸.

67 Here, we isolate the effects of seabird-derived nutrients on adjacent coral reefs using a rare,
68 large-scale natural experiment where some islands in a remote coral reef archipelago are rat-
69 infested, while others are rat-free. The northern atolls of the Chagos Archipelago, central
70 Indian Ocean, have been uninhabited by people for over 40 years, are protected from fishing,
71 and host some of the world's most pristine marine environments¹³. Black rats (*Rattus rattus*)
72 are thought to have been introduced to the archipelago in the late 1700s and early 1800s, but
73 due to patterns of human habitation and movement, are not present on all islands. We use this
74 unique scenario and a mixed-methods approach to investigate nutrient flux between oceanic,
75 island, and coral reef ecosystems.

76 We studied six rat-free and six rat-infested islands, selected to be otherwise similar in terms
77 of size, location and environment. Rats are known to predate upon bird eggs, chicks, and
78 occasional adults, decimating populations where they have been introduced⁸. Mean seabird
79 density, averaged across a 6-year period (Methods), was 760 times greater on rat-free than
80 rat-infested islands (Fig 1a; 1243 birds/ha rat-free, 1.6 birds/ha rat-infested). These high
81 seabird densities on some islands has led to Chagos having ten Important Bird and
82 Biodiversity Areas¹⁴. Biomass of 14 bird species within six families varied among islands,
83 with terns and noddy's contributing greatest biomass, and booby's, shearwaters, and frigate
84 birds only common on some islands. Biomass of all species was greatest on rat-free islands
85 (Fig. 1b).

86 We used species-specific abundance, body size scaled defecation rate, nitrogen content of
87 guano¹⁵, and mean residence times on the islands to estimate mean nitrogen input by the
88 seabirds (Methods). Nitrogen input by seabirds per hectare of island was 251 times greater on
89 rat-free islands than rat-infested islands (Fig 1c; 190 kg/ha/yr rat-free, 0.8 kg/ha/yr rat-
90 infested). The nutrient input onto rat-free islands is comparable to nitrogen inputs by seabirds
91 at the isolated and rat-free Palmyra atoll in the Pacific¹⁵. We did not calculate nutrient input
92 from rats as they are recycling nutrients already present on the islands. In contrast, the
93 majority of the seabirds feed in the open ocean, substantial distances from reefs (Extended
94 Data Table 1). By foraging offshore, seabirds feed from food webs supported by net primary
95 production that is estimated to be 2 to >5 orders of magnitude higher than net primary
96 production on adjacent coral reefs (Methods; Extended Data Figure 1). Their capacity to
97 access these oceanic prey resources leads to substantial deposition of oceanic nitrogen that
98 would otherwise be unavailable on rat-free islands.

99 We used abundance of nitrogen and stable isotopes (reported as $\delta^{15}\text{N}$) to understand uptake of
100 nutrients on islands and in adjacent coral reef ecosystems (Methods; Fig. 2). Abundance and

101 $\delta^{15}\text{N}$ were strongly and positively correlated ($r = 0.96$), meaning that they show similar
102 patterns in our samples. Soils on rat-free islands were enriched in ^{15}N , with $\delta^{15}\text{N}$ being 3.8
103 times higher than on rat-infested islands and comparable to reported values for seabird
104 guano¹⁶ (Fig. 2b). Substantially greater $\delta^{15}\text{N}$ was also evident in new growth leaves of a
105 coastal plant (*Scaevola taccada*) on rat-free islands (Fig. 2c), indicating uptake of oceanic
106 derived nutrients by island vegetation.

107 Nitrogen is expected to leach off islands to nearshore marine environments through rainfall
108 and coastal advection¹¹. On the reef flat (~1 m deep and 100 m from shore) filter feeding
109 sponges (*Spherospongia* sp; Fig 1d) and macroalgae (*Halimeda* sp; Fig 1e) had substantially
110 higher $\delta^{15}\text{N}$ values near rat-free islands, though differences were smaller than observed for
111 island soils and vegetation. This is consistent with findings of higher $\delta^{15}\text{N}$ values in corals
112 closer to seabird colonies in New Caledonia¹⁷. On the reef crest (~3 m deep and 230 m (± 55
113 m StDev) from island shorelines) $\delta^{15}\text{N}$ was significantly higher in turf algae and herbivorous
114 damselfish (*Plectroglyphidodon lacrymatus*) muscle adjacent to rat-free islands (Fig. 2f, g).
115 While recognising the influence of trophic fractionation on $\delta^{15}\text{N}$ signatures, the relative
116 depletion of the heavy isotope ^{15}N from soils across to the reef crest on rat-free islands,
117 compared to the relatively stable values for rat-infested islands, provides strong evidence of
118 seabird-vectored nutrient enrichment propagating out onto adjacent coral reefs. These
119 diminishing effect sizes from the islands out to the reef crest likely reflect a range of
120 processes, including uptake and conversion of nitrogen by micro- and macro-organisms
121 across the reef flat¹⁸.

122 Comparison of damselfish growth on reef crests (using growth bands in otoliths; Methods)
123 demonstrated that individuals adjacent to rat-free islands were growing significantly faster
124 towards their maximum expected size ($K_r - K = -0.10 [-0.18, -0.04]$, net rat effect), and were
125 larger for a given age than individuals on reefs adjacent to rat-infested islands (Fig. 3). This is

126 the first evidence for seabird-vectored nutrient subsidies propagating through the food web to
127 accelerate the growth of a marine vertebrate. Given the diversity and high biomass of fishes
128 that feed on benthic algae on coral reefs¹⁹, this finding is likely to indicate higher fish
129 production adjacent to seabird dominated islands with repercussions for production of their
130 predators.

131 To assess the influence of seabird colonies on reef fish biomass production, we surveyed fish
132 communities along reef crests of the islands (Methods). Total biomass of the reef fish
133 community was 48% greater adjacent to rat-free islands. Assigning the 123 species of reef
134 fish recorded into feeding groups, we found biomass to be greater for all feeding groups of
135 fish on reefs adjacent to rat-free islands, with herbivore biomass having the largest effect size
136 (93% of posterior distribution above zero; Fig. 4a). These results are consistent with seabird-
137 vectored nutrients subsidising the entire ecosystem.

138 Herbivorous fish are functionally important on coral reefs, maintaining a healthy balance
139 between corals and algae, and clearing space for coral settlement²⁰. Parrotfishes are among
140 the most abundant and important herbivorous groups, providing unique grazing and
141 bioerosion functions. We estimated grazing and bioerosion rates of parrotfishes for each
142 island using density data, along with species- and body size-specific information on
143 consumption rates²¹ (Methods). Reef crests adjacent to rat-free islands are fully grazed 9
144 times a year, compared to 2.8 times for rat-infested islands (median values; Fig. 4b;
145 $\text{Grazing}_{\text{rats}} - \text{Grazing}_{\text{no rats}} = -1.18 [-2.24, -0.11]$, net rat effect). Although variable, median
146 bioerosion rates were 94 tonnes/ha/yr adjacent to rat-free islands, 3.8 times higher than the
147 24.5 tonnes/ha/yr adjacent to rat-infested islands (Fig. 4c; $\text{Erosion}_{\text{rats}} - \text{Erosion}_{\text{no rats}} = -1.06 [-$
148 $2.77, 0.53]$, net rat effect). Bioerosion is critical for breaking down dead substratum between
149 major disturbance events to provide stable substratum for new coral growth and recovery²⁰,
150 and for providing sand to maintain island growth in low lying atolls²². While some

151 bioeroding parrotfishes can take bites from corals, coral cover was not lower on rat-free
152 islands (coral cover rat-free = $26.3\% \pm 5.2$ SE; rat-infested = 28.2 ± 5.5 SE). These data are
153 consistent with seabirds on rat-free islands enhancing key ecosystem functions on coral reefs.
154 Following our surveys, coral reefs of the Chagos Archipelago lost ~75% coral cover in the
155 2016 El Niño driven mass coral bleaching event²³. It is possible that corals surrounding rat-
156 free islands will show greater resilience to this event than corals adjacent to rat-infested
157 islands, for two key reasons. Firstly, in contrast to nutrient inputs from anthropogenic
158 sources, nutrient delivery from biological sources such as fish and seabirds is rich in
159 phosphorus^{3,24} which has been shown to enhance coral thermo-tolerance²⁵ and coral
160 calcification rates²⁴. Secondly, greater grazing rates, as observed on reefs adjacent to rat-free
161 islands, is a key determinant of reef recovery²⁶.

162 Here, we have shown that seabird nutrient subsidies fuel the coral reef ecosystem, reflecting
163 natural productivity and functioning in the absence of introduced rats. Oceanic coral reefs,
164 such as those in the Chagos Archipelago, are highly productive ecosystems in an oligotrophic
165 environment, the mechanism of which has intrigued scientists for decades²⁷. Seabird vectored
166 nutrient subsidies are clearly a major pathway through which this productivity is supported,
167 and such subsidies should be considered in the design and analyses of coral reef surveys
168 adjacent to oceanic islands.

169 Rat eradication has been successful on 580 islands worldwide, and although success rates are
170 slightly lower for tropical islands (89%) compared to temperate (96.5%), new techniques and
171 guidelines are expected to close this gap²⁸. As eradication of rats from islands can lead to
172 immigration and positive growth rates of seabird populations²⁹, rat removal should be a
173 conservation priority for coral reef islands. The return of seabirds would benefit not only the
174 island ecosystem, but also adjacent nearshore marine ecosystems. In a time of unprecedented

175 threats to coral reefs from climate change³⁰, enhancing productivity and key ecosystem
176 functions will give reefs the best possible chance to resist and recover from future
177 disturbances.

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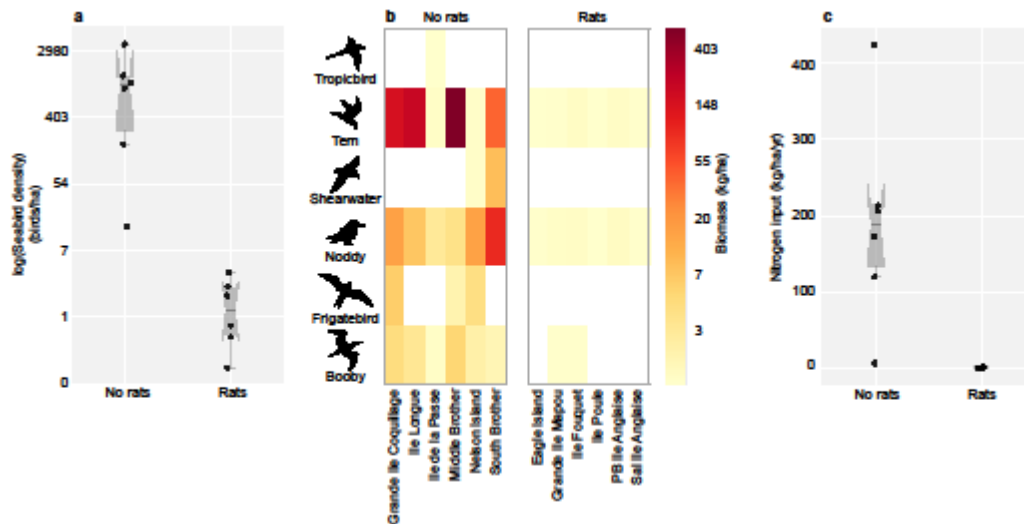
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267
268 **Author Contributions** N.A.J.G. conceived of the study with S.K.W.; N.A.J.G., S.K.W., and
269 P.C. collected the data; N.A.J.G., M.A.M, S.J., and A.S.H. developed and implemented the
270 analyses; N.A.J.G. led the manuscript with S.K.W., M.A.M., S.J., A.S.H., and P.C.

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272 **Author Information**

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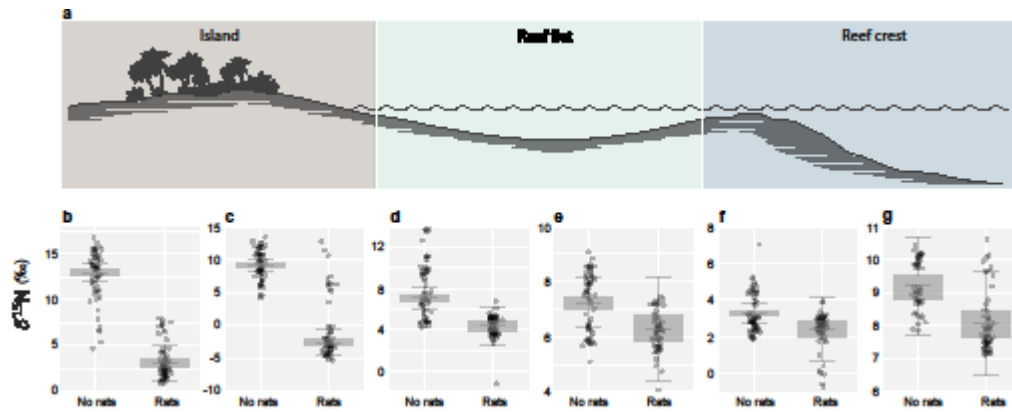
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308 **Figure 1 | Seabird densities, biomass, and nitrogen input to islands with and without**
 309 **rats in the Chagos Archipelago.** a) Seabird density on rat-free (n = 6) and rat-infested (n =
 310 6) islands. b) Heatmaps of seabird biomass per family, on each island. Tropicbird: *Phaethon*
 311 *lepturus*; Tern: *Thalasseus bergii*, *Sterna sumatrana*, *Sterna dougallii*, *Onychoprion*
 312 *fuscatus*, *Onychoprion anaethetus*, *Gygis alba*; Shearwater: *Puffinus bailloni nicolae*,
 313 *Ardena pacifica*; Noddy: *Anous tenuirostris*, *Anous stolidus*; Frigatebird: *Fregata sp.*;
 314 Booby: *Sula sula*, *Sula leucogaster*. c) Nitrogen input by seabirds per hectare for rat-free (n =
 315 6) and rat-infested (n = 6) islands. Panels a) and c) are notched box plots, where the
 316 horizontal line is the median, box height depicts the interquartile range, whiskers represent
 317 95% quantiles, and diagonal notches illustrate approximate 95% confidence intervals around
 318 the median. Estimated net rat effects (median [95% highest posterior density intervals]) are a)
 319 456 [22, 6393] birds/ha; b) 195 [184, 207] kg/ha (total biomass); and c) 148 [81, 211]
 320 kg/ha/yr.

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330 **Figure 2 | Nitrogen isotope signals from islands to reefs in the presence and absence of**
 331 **invasive rats.** a) Schematic of study system. $\delta^{15}\text{N}$ values for b) soil, and c) new growth
 332 leaves (*Scaevola taccada*) on islands, d) filter feeding sponges (*Spheciospongia* sp), and e)
 333 macroalgae (*Halimeda* sp.) on reef flats, and f) turf algae, and g) dorsal muscle tissue of
 334 damselfish (*Plectroglyphidodon lacrymatus*) on reef crests. For all samples, n = 120 were
 335 collected, except for panel g), where n = 110 (Methods). Panels b-g are box plots, where the
 336 horizontal line is the median, box height depicts first and third quartiles and whiskers
 337 represent the 95th percentile. Net rat effect (median [95% highest posterior density] and
 338 P(neg), the probability of effect being less than zero) estimates are b) soil -9.9 [-11.3, -8.4]
 339 P(neg)>0.99; c) leaves -11.8 [-13.2, -10.2] P(neg)>0.99; d) sponge -1.0 [-2.3, 0.5] ,
 340 P(neg)=0.92; e) macroalgae -2.7 [-4.1, -1.23] P(neg)>0.99; f) turf -0.8 [-2.23, 0.6]
 341 P(neg)=0.90; g) fish -1.1 [-2.5, 0.3] P(neg)=0.94.

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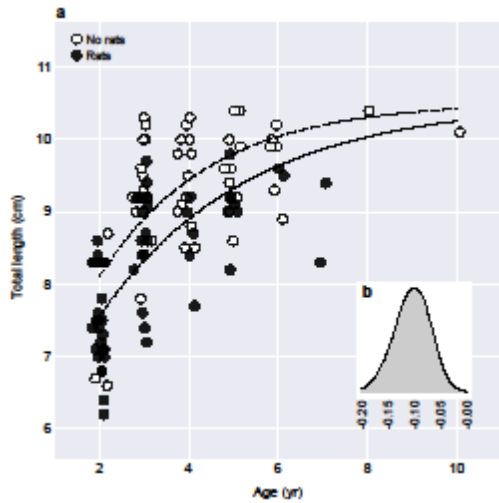
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357 **Figure 3 | Growth of herbivorous damselfish on coral reefs adjacent to islands with and**
 358 **without rats.** a) Age by length growth curves for *Plectroglyphidodon lacrymatus* on rat-free
 359 (open circles) and rat-infested (closed circles) islands. b) Effect size posterior density for the
 360 difference between the growth parameter, K (yr^{-1}), on rat-free compared to rat-infested
 361 islands. $n = 48$ rat-free, and $n = 58$ rat-infested biologically independent samples.

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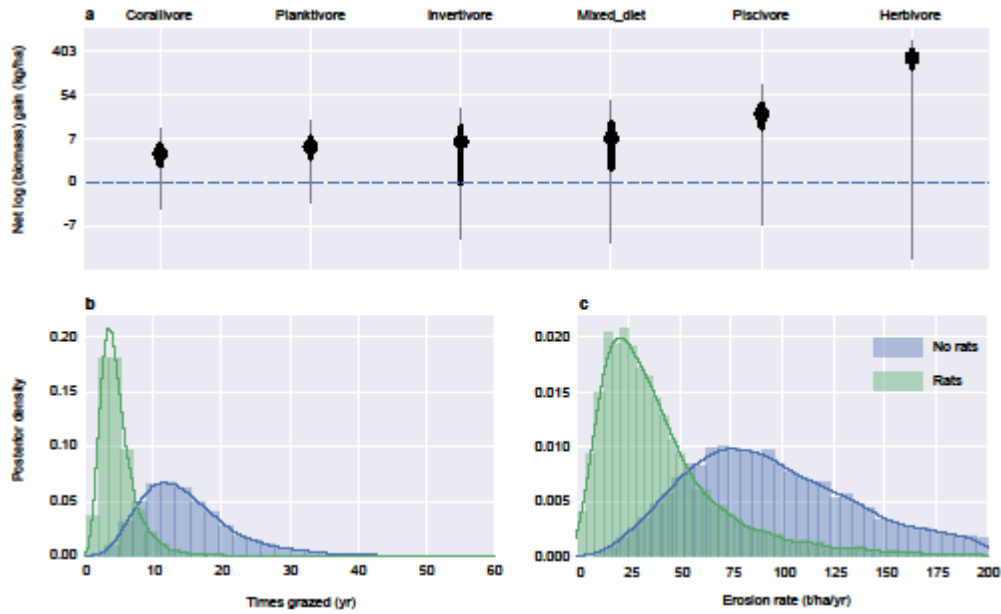
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379 **Figure 4 | Biomass and functioning of reef fish communities adjacent to islands with and**
 380 **without rats.** a) Effect size plots from a hierarchical Bayesian analysis of fish biomass for
 381 different feeding groups between rat-free and rat-infested islands. n = 24 rat-free, and n = 24
 382 rat-infested biologically independent surveys. Circles represent means, and dark and grey
 383 bars represent 50% and 95% uncertainty intervals, respectively (highest posterior density).
 384 Positive values correspond to greater biomass on rat-free islands. b) Effect size posterior
 385 density distributions for the proportion of reef grazed by parrotfishes each year on islands that
 386 are rat-free versus rat-infested. c) Effect size posterior density distributions for the volume of
 387 reef carbonate removed by parrotfishes each year on rat-free versus rat-infested islands.

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397 **METHODS**

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399 **Study sites.** The Chagos Archipelago (British Indian Ocean Territory) is situated in the
400 central Indian Ocean, due south of the Maldives (5° 50' S, 72° 00' E). The archipelago was
401 first discovered in the early 1500s, but was not settled until the 1700s, after which rats were
402 inadvertently introduced to some islands of the territory³¹. In the early 1970s the British
403 government established a lease of the southernmost atoll (Diego Garcia) to the US Navy for a
404 military base, and resettled the Chagossian people in Mauritius, Seychelles, and the UK.
405 Since that time, the atolls of the northern archipelago have had very few direct human
406 impacts³², with exceptionally high reef fish biomass³³, very low levels of water pollution³⁴,
407 and there are currently 10 designated (2 more proposed) Important Bird and Biodiversity
408 Areas¹⁴. However, invasive rats remain on a number of islands, creating a natural experiment
409 to study the influence of rats on relatively undisturbed oceanic islands. In March-April 2015,
410 we conducted research at 12 islands of similar size, across three atolls (Extended Data Table
411 2). Six of the islands were chosen as they are rat-free, while the other six are rat-infested.

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413 **Seabird surveys.** Breeding seabird densities on each island were counted annually by P.C.
414 from 2009-2015 using the apparently occupied nests methodology (AONs)^{35,36}. The entire
415 coastline of each island was surveyed first and AONs directly counted. Following the coastal
416 survey, the interior of the island was searched. There were no breeding seabirds in the interior
417 of Ile Poule, Grand Ile Mapou, Ile Fouquet, Eagle Island, and both Ile Anglaise islands. On
418 islands where the interior search revealed breeding seabirds, techniques to estimate AONs
419 varied by family. Brown Booby (*Sula leucogaster*) AONs were directly counted. Red-footed
420 Booby (*Sula sula*) AONs were counted directly except on Nelson Island, and Grand Ile
421 Coquillage. On these islands the total surface area of the breeding population was calculated

422 using a handheld Global Positioning System (GPS) and random plots of the area were
423 counted for AONs. Plot size and whereabouts was directed by accessibility, visibility and the
424 vulnerability of the breeding population. The means of the AONs of the plots were multiplied
425 by the number of plots possible in the mapped area to estimate total AONs. Breeding
426 frigatebirds (*Fregata sp.*) on Nelson Island and Grand Ile Coquillage were estimated using
427 the same technique described above for Red-footed Booby. No tropicbird (*Phaethon*
428 *lepturus*) nesting cavities were located, so tropicbird breeding numbers were estimated by
429 counting aerial displaying pairs above islands or nest-prospecting adults in an appropriate
430 habitat. Shearwaters (Procellariidae) nest in burrows, with the largest colony on South
431 Brother island and some also on Nelson Island. Burrows is a loose term that covers rock
432 fissures, crevices, tree roots, coconut boles, and various underground holes. Island surface
433 area where burrows are present was estimated and AONs estimated by multiplying from an
434 average burrow density, taken from random 10 m² sample plots throughout the island.
435 Burrows were assumed occupied when a bird or egg was seen in them, there were indications
436 of use (e.g. feathers, droppings), or they were heavily scented with shearwater musk. Burrows
437 were assigned to either one of the shearwater species by identification of large chicks, eggs,
438 or adults. For the arboreal breeding Noddy's (*Anous spp.*), direct counts were impractical for
439 the large colonies on South Brother and Nelson Island, where subsampling and multiplication
440 to the total colony area was used. All ground nesting tern species (Sternidae) with the
441 exception of Sooty Tern (*Onychoprion fuscatus*) had AONs directly counted. To calculate the
442 number of Sooty Tern AONs, the total colony area was mapped and random sample plots
443 were counted for AONs to multiply up to the total area. Plot size was dictated by
444 accessibility, visibility, and to avoid disturbing dense aggregations of breeding birds, with
445 numbers counted from outside the colony at random points around the perimeter. While
446 vegetation type, such as coconut versus native forests, can also affect bird densities¹⁵, much

447 of the indigenous island vegetation has been lost in Chagos¹⁴, and we used absolute bird
448 count estimates per island for this study.

449

450 Total annual seabird abundance was calculated based on the number of AONs multiplied by
451 the mean number of birds occupying those nests per species, and the period of the year that
452 the birds are present on the islands. For most species, a conservative 3 birds per nest was used
453 (2 adults and 1 chick), but some, for example sooty terns (*Onychoprion fuscatus*) have 1
454 adult, or 1 adult and 1 chick present for periods of the year, and others (e.g. red-footed booby
455 (*Sula sula*)) have a chick and 1-2 juvenile/immature birds present in the nest or sub-colony
456 area. Period of year spent on the island varied by species, from year round for species such as
457 the brown booby (*Sula leucogaster*) and common white tern (*Gygis alba*), to 4 months for the
458 roseate tern (*Sterna dougallii*). Biomass of bird species was estimated using the average mass
459 of an individual of each species taken from the Handbook of the Birds of the World³⁷.

460

461 We estimated the total nitrogen input from guano per hectare per year of each island
462 following Young et al. (15):

463

464

$$465 \quad NI_{ij} = \frac{Ng \times Dr_i \times Bd_{ij} \times Res_{ij}}{IsArea_j}$$

466

467

468 where nitrogen input per hectare per year (NI) is estimated from the nitrogen content of
469 guano (Ng), the defecation rate in g per species of bird (i) per day (Dr), the number of that
470 species of bird (Bd) on the island (j), the number of days of the year that the species is
471 resident on the island (Res), and the area of the island ($IsArea$). Following (15), nitrogen
472 content of guano was held at 18.1% based on guano samples from similar species in the

473 Pacific. The contribution of guano (g) was based on the red-footed booby and scaled for other
474 species based on species biomass, assuming allometric relationships with body size¹⁵. We
475 adjusted the *Bd* estimates to account for time off islands during feeding forays. Given
476 uncertainties in foraging durations and whether birds would have full crops and bowels, it is
477 hard to be completely precise in these calculations. We assigned the 14 species into 3 groups,
478 which accounts for foraging excursions off island in a fairly conservative way. Group 1:
479 *Tropical shearwater, wedge-tailed shearwater, white-tailed tropicbird, sooty tern, brown*
480 *noddy, and frigatebirds*. Foraging will vary during the breeding cycle, but often one adult is
481 foraging and may be off the island overnight. We therefore assumed only one adult of the
482 pair was on the island at any one time. Group 2: *Red-footed booby*. One bird of the pair
483 makes daylight foraging forays but returns overnight. Adult numbers were therefore halved
484 only during daylight hours (12 hours). Group 3: *Great crested tern, roseate tern, black-naped*
485 *tern, common white tern, bridled tern, brown booby, lesser noddy*. In Chagos, these species
486 tend to make much shorter foraging forays (1-4 hours depending on species), meaning
487 defecation at sea will be minimal compared to land. We therefore did not make any
488 adjustments to their numbers.

489

490 Seabird densities per hectare of rat-free versus rat-infested islands were plotted as notched
491 box plots, where the horizontal line is the median, box height depicts the interquartile range,
492 and diagonal notches in the boxes illustrate the 95% confidence interval around the median³⁸.
493 The biomass of families of birds per island were plotted as log-scale heat maps for rat-free
494 and rat-infested islands. Nitrogen input for rat-free versus rat-infested islands were plotted as
495 notched box plots of kg per hectare per year. We also developed a set of simple Bayesian
496 models to estimate the net rat effects on log-scale bird numbers, log-scale total biomass, and
497 nitrogen input between rat-free and rat-infested islands:

498
$$y_i \sim N(\mu_i, \sigma_t)$$

499
$$\mu_i = \beta_0 + \beta_1 * RAT$$

500
$$\beta_x \sim N(0,10)$$

501
$$\sigma_t \sim U(0,10)$$

502 where y_i was the response variable, RAT was a dummy variable for rat-infested islands, and
503 variances were estimated independently within treatments. The β_1 parameters being the rat
504 effect sizes reported in the caption of Figure 1 along with the proportion of β_1 posterior
505 density below zero.

506

507 **Primary production and potential prey biomass and production available to seabirds.**

508 Biomass, production, and size-structure of consumers in the ocean surrounding the Chagos
509 Islands were calculated from the primary production available to support them using a size-
510 based model that characterises some of the main factors affecting the rate and efficiency of
511 energy processing in marine ecosystems³⁹. Briefly, these factors are (i) temperature, which
512 affects rates of metabolism and hence growth and mortality; (ii) the size of phytoplankton and
513 the predator to prey body mass ratio, which determine the number of steps in a food chain;
514 and (iii) trophic transfer efficiency, a measure of energy conserved and lost at each step in the
515 chain. In the model, size composition of the phytoplankton community is predicted from
516 primary production and temperature using empirical relationships and, in turn, this size
517 composition is used to estimate particle export ratios that influence transfer efficiency in the
518 first steps of the food chain. The model is depth integrated and we made the simplifying
519 assumption that all primary production occurs in the euphotic zone. We did not explicitly
520 model production of benthic communities, but these would not be accessible to seabirds.
521 In the model, relationships between primary consumer production and consumer production
522 at any higher trophic level are determined by trophic transfer efficiency. Production at a

523 given body mass or trophic level was converted to biomass and numbers at the same body
524 mass or trophic level based on the assumption that body size and temperature determined
525 individual rates of production³⁹. The modelled size-spectrum was discretised into units of 0.1
526 (\log_{10}) for analysis.

527

528 The environmental data used to force the models comprised annual mean estimates of depth
529 integrated primary production ($\text{g C m}^{-2} \text{d}^{-1}$) and sea surface temperature ($^{\circ}\text{C}$) as derived from
530 monthly predictions for the years 2010- 2012. Chlorophyll and primary production were
531 obtained from the Mercator Ocean Project (Global Biogeochemical Analysis Product ,
532 BIOMER1V1 monthly 0.5° degree resolution)⁴⁰ and monthly temperature data from the
533 Mercator Ocean physical NEMO model (PSY3V3R1)⁴¹. Inputs to the size-based models were
534 allocated to a 0.5° grid that covered the sea area defined by the maximum foraging distance
535 of the species of seabird, assumed to be a radius, such that foraging areas were circular
536 around the islands (Extended Data Table 1). These distances are an approximation from the
537 published literature, given foraging ranges can vary geographically⁴². Cells were assigned a
538 mixed layer depth (m) and total depth (m)^{43,44}. Mean biomass and production for organisms
539 in body mass (wet weight) classes 0.1-9 g (smaller prey) and >1-50 g (larger prey) was
540 estimated per unit area by grid cell, to approximate size ranges consumed by the seabird
541 species based on prey size information in the literature and body mass class^{45,46}. To address
542 considerable uncertainty in model parameters, we ran 10000 simulations for each biomass or
543 production estimate in each grid cell, with parameter estimates in each simulation drawn
544 randomly from appropriate distributions. When parameters were correlated, the parameter
545 estimates were drawn from multivariate distributions³⁹. Model results were expressed as
546 medians and percentiles calculated from the distribution of output values. Conversions from
547 carbon to wet weight were based on published values^{39,47}. Estimates of nitrogen content in

548 prey size classes were based on an assumed C:N ratio of 3.4:1, which is a typical value for
549 fish⁴⁸ and reflects the falling C:N ratio with trophic level in food webs that are supported by
550 primary producers with C:N ratios typically averaging 6.6:1 (ref. 49,50). Estimates of
551 biomass and production per unit area were converted to estimates of total biomass or
552 production in the foraging area of each bird species (Extended Data Table 1, Extended Data
553 Figure 1).

554

555 While rates of gross primary production can be high on coral reefs, net primary production,
556 although variable in space and time, is typically comparable with net primary production in
557 the more productive areas of the tropical ocean^{51,52}. Given the area of reef surrounding the
558 rat-free islands is approximately 1.02 km², while foraging areas are >105 km² for 14 of the 15
559 bird species using these islands, large numbers of seabirds can feed from oceanic food webs
560 with much higher production than those on the reefs (Extended Data Figure 1). Even the
561 production estimates for prey in the size-ranges eaten by the seabirds are typically 3 or more
562 orders of magnitude higher than the expected primary production on this area of reef (0.0001
563 Tg C yr⁻¹, if mean on-reef primary production is assumed to be 0.3 g C m⁻² d⁻¹)⁵¹. Given the
564 numbers of seabirds and the extent of the prey resource they have the potential to access, the
565 strong signal from guano derived nitrogen on the reefs surrounding rat-free islands is
566 unsurprising. While the model has a number of assumptions, the results do highlight that
567 oceanic production in the foraging area is expected to be several orders of magnitude higher
568 than production on the reefs surrounding the islands and therefore that the higher levels of
569 connectivity that result from higher seabird abundance have the potential to transport
570 relatively high quantities of nitrogen to the reef systems.

571

572 **Isotope sampling.** From each island, 10 samples of topsoil (<5 cm from surface) were taken
573 from just behind the coastal vegetation boundary. Loose leaf litter and other vegetation was
574 cleared to expose the soil, and samples were taken a minimum of 10 m apart. Along the
575 beach margin of each island, new growth leaf samples were taken from 10 *Scaevola taccada*
576 plants. On the reef flat of each island, ~1 m deep and approximately 100 m from shore, 10
577 samples of filter feeding sponges (*Sphaciospongia* sp.) and macroalgae (*Halimeda* sp.) were
578 taken from individual colonies and thalli, respectively. On the reef crest of each island, ~3 m
579 deep and 230 m (\pm 55m StDev) from shore, 10 turf algal samples were taken from dead
580 corals. Ten territorial herbivorous damselfish (*Plectroglyphidodon lacrymatus*) individuals
581 were collected by hand spear on the reef crest of each island in the same area the turf algae
582 were collected. Fish were euthanized on ice. Fish samples could not be collected from Nelson
583 Island. A sample of dorsal white muscle was taken from each fish. All samples were dried in
584 a drying oven at 60°C for 24 hours or until fully dry. Samples were powdered with a pestle
585 and mortar and stored in sealed plastic sample vials.

586

587 Stable isotope analysis of nitrogen for all samples was carried out at the University of
588 Windsor, Canada. Isotope ratios were calculated from 400 to 600 μ g of each sample added to
589 tin capsules and analysed with a continuous flow isotope ratio mass spectrometer (Finnigan
590 MAT Deltaplus, Thermo Finnigan, San Jose, CA, USA). Total nitrogen content (%) was also
591 estimated. Stable isotope values for nitrogen are expressed as delta (δ) values for the ratio of
592 $^{15}\text{N}:^{14}\text{N}$. Turf, sponge, soil and macroalgae samples were acid washed with hydrochloric acid
593 to dissolve any calcareous matter or sediments that may have contaminated the samples.
594 Subsets of samples that were run with and without the acid wash had correlation coefficients
595 between 0.9 (turf) and 0.99 (soil), and all samples from rat-free and rat-infested islands were
596 treated the same. The standard reference material was atmospheric nitrogen. Samples were

597 run twice, with select samples run in triplicate to ensure accuracy of readings. Accuracy was
598 within 0.3 ‰ for soil and within 0.1 ‰ for other samples, based on soil Elemental
599 microanalysis B2153 and USGS 40 internal standards, respectively.

600

601 $\delta^{15}\text{N}$ values between rat-free and rat-infested island treatments were analysed using Bayesian
602 hierarchical models, with area of reef surrounding each island (RA; calculated using GIS) as
603 a covariate, and samples nested within their specific atoll. Distance to shore from the reef
604 crest (DS) was used as an additional covariate for the turf algae and fish muscle samples.
605 Models were run using the PyMC3 package⁵³ in Python (www.python.org), including a t-
606 distribution with $df=4$ as:

607

608

$$609 \quad \delta^{15}N_{oij} \sim t_4(\mu_{oij}, \sigma_0)$$

$$610 \quad \mu_{oij} = \beta_{0i} + \beta_{1o} + \beta_{2o}RA + \beta_3DS$$

$$611 \quad \beta_{0i} \sim N(\gamma_0, \sigma_\gamma)$$

$$612 \quad \beta_x, \gamma_0 \sim N(0, 1000)$$

$$613 \quad \sigma_0, \sigma_\gamma \sim U(0, 100)$$

614

615 where each organism (o) had their own offset (β_1) relative to island-level (i) soil intercepts
616 (β_0). Models were examined for convergence and fit by consideration of stability in posterior
617 chains, Gelman-Rubin (R-hat) statistics, and the fit of the models with the data⁵⁴. A gist of
618 the PyMC3 code used for the $\delta^{15}\text{N}$ model is available at:

619 <https://gist.github.com/mamacneil/42a426997b73b6283d3e50bc1c95a9a9>

620

621 **Fish growth.** The total length of each damselfish (*Plectrogllyphidodon lacrymatus*) sampled
622 was carefully measured to the nearest mm. The paired sagittal otoliths (ear bones) were
623 removed from each individual to estimate age⁵⁵. One otolith from each pair was weighed to
624 the nearest 0.0001 g and affixed to a glass slide using thermoplastic glue with the primordium
625 located just inside the edge of the slide and the sulcul ridge perpendicular to the slide edge.
626 The otolith was ground to the slide edge using a 600 grit diamond lapping disc on a grinding
627 wheel along the longitudinal axis. The otolith was then removed and re-affixed to a clean
628 slide with the flat surface against the slide face and ground to produce a thin transverse
629 section c. 200 μm thick, encompassing the core material. Finally, the exposed section was
630 covered in thermoplastic glue to improve clarity of microstructures. Sections were examined
631 twice and age in years was estimated by counting annuli (alternating translucent and opaque
632 bands) along a consistent axis on the ventral side of the sulcul ridge, using transmitted light
633 on a stereo microscope.

634

635 Growth curves for the otoliths from the rat-free versus rat-infested islands were modelled
636 using the three-parameter van Bertalanffy growth function, implemented in PyMC3 as:

637

638

$$\log(L_t) \sim N(\mu_i, \sigma_0)$$

639

$$\mu_i = \log(L_\infty - (L_\infty - L_0)e^{-(k_0+k_1)t})$$

640

$$k_0 \sim U(0.001, 1)$$

641

$$k_1 \sim N(0, 10)$$

642

$$L_0 \sim N(0, \text{min}L)$$

643

$$L_\infty \sim U(\text{max}L, \text{max}L \times 2)$$

644

$$\sigma_0 \sim U(0, 1000)$$

645

646 Where L_t is the observed total length (cm) at age t (years), L_∞ is the estimated asymptotic
647 length, K is the coefficient used to describe the curvature of growth towards L_∞ (here split
648 into k_0 (no rats) and k_1 (rat offset)) and L_0 is the theoretical length at age zero⁵⁶. We specified
649 uniform bounds for the L parameters based on observed minimum ($minL=6.2$) and maximum
650 ($maxL=10.4$) fish lengths. Again, models were examined for convergence and fit by
651 consideration of stability in posterior chains, R-hat statistics, and the fit of the models with
652 the data. A gist of the PyMC3 code used for the von Bertalanffy model is available at:
653 <https://gist.github.com/mamacneil/6970e4ff88768532635dd44a682f7b9d>

654

655 **Fish biomass and function.** Underwater visual surveys were conducted along the reef crest
656 of each island. Four 30 m transects were laid along the reef crest at 3 m depth, separated by at
657 least 10 m. Benthic cover of corals, algae, and other organisms were surveyed using the point
658 intercept method, whereby the substratum type under the transect tape every 50 cm was
659 recorded. The structural complexity of the reef was estimated visually on a 6 point scale,
660 ranging from no relief to exceptionally complex (>1 m high) relief with numerous caves and
661 overhangs. This structural complexity measure captures landscape complexity, including the
662 complexity provided by live corals, that of the underlying reef matrix and other geological
663 features, and has been shown to correlate well to other measures of complexity, such as
664 measures of reef height and the linear versus contour chain method⁵⁷. The density and
665 individual sizes of diurnally active, non-cryptic species of reef-associated fish were estimated
666 along each transect. Larger, more active fish were surveyed on the first pass of each transect
667 in a 5 m wide belt, while the more territorial and abundant damselfish family
668 (Pomacentridae) were surveyed on a second pass of the transect in a 2 m wide belt. We
669 converted data on fish counts to biomass with published length–weight relationships^{58,59}. Fish
670 were assigned to feeding groups based on their dominant diets and feeding behaviour⁶⁰.

671

672 The grazing and erosion potential (i.e. area of reef scraped, and volume of carbonates
673 removed, respectively) by parrotfishes at each site was calculated as the product of feeding
674 rate, bite dimension (area or volume), and fish density (following²¹). Size-specific feeding
675 rates for each species were derived from best-fit regressions of bite rate (bites min⁻¹) and fish
676 length (total length, cm) for each species. Bite rates were quantified at three locations (Lizard
677 Island, northern Great Barrier Reef, northern Sumatra, Indonesia, and the central Red Sea)
678 using focal feeding observations. An individual parrotfish was haphazardly selected, followed
679 for a short period of acclimation (~1 min) during which the fish length (total length, TL) was
680 estimated to the nearest centimetre. Following the acclimation period each fish was followed
681 for a minimum of 3-minutes during which the number of bites on different benthic substrata
682 (primarily epilithic algal matrix and live corals) and observation time was recorded. Bite rates
683 were then converted to bites min⁻¹. Observations were discontinued if the focal individual
684 displayed a detectable response to the diver. All feeding observations were conducted during
685 0900-1500h with a minimum of 25 observations conducted per species per location.

686 The area (mm²) and volume (mm³) of material removed per bite by individual parrotfish was
687 estimated from species-specific relationships between bite size and fish length. To estimate
688 bite area an individual parrotfish was haphazardly selected, its total length estimated and
689 followed until it took a bite from the reef substratum. The dimensions of the bite (length and
690 width) were then measured in situ using dial callipers. A minimum of 16 observations (mean
691 = 34.3 observations) were made per species, with all observations performed at Lizard Island,
692 northern GBR. Bite volumes of species were largely taken from the literature⁶¹, and
693 supplemented with in situ observations at Lizard Island for *Chlorurus microrhinos*. Where
694 possible species-specific bite rates and bite dimensions were used, when these were not
695 available, values for closely related congeners were used.

696 Total biomass and biomass of each trophic feeding group of fish (BIO_f) was modelled using
 697 Bayesian hierarchical models, with observations (j) nested within atolls (i) and including
 698 factors that could influence fish biomass as covariates; coral cover (HC), reef structural
 699 complexity (SC), and distance to shore (DS). The general model was:

700

701

$$\log(BIO_{fij}) \sim N(\mu_{fi}, \sigma_0)$$

702

$$\mu_{fi} = \beta_{f0i} + \beta_1 RAT + \beta_2 SC + \beta_3 HC + \beta_4 DS$$

703

$$\beta_{f0i} \sim N(\gamma_{f0}, \sigma_\gamma)$$

704

$$\beta_x, \gamma_{f0} \sim N(0, 1000)$$

705

$$\sigma_0, \sigma_\gamma \sim U(0, 100)$$

706

707 with models examined for convergence and fit by consideration of stability in posterior
 708 chains, R-hat statistics, and the fit of the models with the data. A gist of the PyMC3 code
 709 used for the fish biomass models is available at:

710

<https://gist.github.com/mamacneil/b8025fe7805d2a86930eda056d60a9a8>

711

712 The two ecosystem functions, grazing and erosion potential (rounded to nearest whole
 713 number), were modelled with the same Bayesian hierarchical structure, but with an
 714 alternative Poisson (Pois) rate (XR) likelihood:

715

716

$$XR_{ij} \sim Pois(e^{\mu_{ji}})$$

717

$$\mu_{ji} = \beta_{j0i} + \beta_1 RAT + \beta_2 SC + \beta_3 HC$$

718

$$\beta_{j0i} \sim N(\gamma_{j0}, \sigma_\gamma)$$

719

$$\beta_x, \gamma_{j0} \sim N(0, 1000)$$

720

$$\sigma_0, \sigma_\gamma \sim U(0, 100)$$

721

722 A gist of the PyMC3 code used for the grazing model is available at:

723 <https://gist.github.com/mamacneil/884836392f4b09efc7f7daf67a73e02f>

724

725 A gist of the PyMC3 code used for the erosion model is available at:

726 <https://gist.github.com/mamacneil/3cbea63ad422e55120a0744acc836ac7>

727

728 Graphics

729 A gist of the Python code used for data summaries and graphics is available at:

730 <https://gist.github.com/mamacneil/f55d48278a8ba4073983b7e2b4ab0e06>

731

732

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839 **Data availability statement**

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841 Data used for figures 1-4 in this paper are available through the GitHub links in the Methods.

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843 **Code availability**

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845 Code used for figures 1-4 in this paper are available through the GitHub links in the Methods.

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850 **Extended Data Figure 1 | Primary production and potential prey biomass and**
851 **production in areas accessible to seabirds foraging around the Chagos Islands.** a)
852 recorded foraging ranges for seabird species that feed on smaller prey (light tone, 0.1 to 9 g
853 individual wet weight) or larger prey (dark tone, 1 to 50 g individual wet weight; broken lines
854 indicate greater ranges are expected for two species and foraging area calculations assume the
855 foraging range is the radius of the foraging area), b) primary production in the foraging area,
856 c) modelled biomass, and d) production of fauna in the foraging area (median and 90%
857 uncertainty intervals based on 10,000 simulations to assess the effects of parameter
858 uncertainty³⁹ on biomass or production estimates). Biomass and production were estimated
859 for fauna in the prey size ranges consumed by each bird species, and expressed as wet or
860 nitrogen (N) weight.